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Top-down and Bottom-up processes during Observation: Implications for Motor Learning

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Abstract

Neurophysiological and behavioural research has linked observational practice to a mirroring mechanism encompassing the action-observation network (AON). Although the original findings indicate that biological stimuli alone activate the AON, recent evidence has shown sensitivity to non-biological stimuli. Thus, the AON is suggested to be influenced by interacting bottom-up and top-down processes. In this review, we describe the multi-functional properties of the AON, and discuss the implications for observational practice and subsequent motor learning.

Keywords: *Observational practice, motor learning, action-observation network*

Introduction

Observational practice (OP) is a process by which humans learn motor skills by observing a model, and has been examined using behavioural and neurophysiological paradigms. The former typically requires an observer to watch a [yoked] model physically performing a novel movement task, after which the learner attempts to imitate the action they have just observed. Despite the absence of explicit involvement of the motor system in trial and error learning during OP, data indicate similar motor learning to those who engage in physical practice. This OP effect is not merely limited to the acquisition of behaviours associated with automatic imitation (see Heyes, 2011), but novel motor skills not already represented in an individual's motor repertoire. Indeed, measures of learning following OP include: absolute and relative (Blandin, Lhuisset, & Proteau, 1999) time; inter-and intra-limb transfer of timing information (Hayes, Andrew, Elliott, Roberts, & Bennett, 2012); spatio-temporal properties of cyclical upper-limb tasks (Vogt, 1995); complex sequence knowledge (Bird & Heyes, 2005); force dynamics (Mattar & Gribble, 2005; Ong & Hodges, 2010); movement kinematics (Hayes, Timmis, & Bennett, 2009).

The majority of the aforementioned behavioural effects have been linked to the general assumption that action-observation and motor-execution are underpinned by a common representational system (e.g., Prinz, 1997). Importantly, however, there is still no widely accepted theory that explains how novel motor skills are acquired during observation. For instance, it was originally thought that higher-level intermediary processes were involved in translating the observed visual stimulus into a motor representation/command (e.g., symbolic coding - Bandura, 1986; amodal processing - Meltzoff & Moore, 1997). More recently, it has been suggested that novel representations developed through imitation learning are associated with sensorimotor transformations that directly recruit the motor system (e.g., mirror-neuron system – Buccino et al., 2004; action-observation network – Cross, Kraemer, Hamilton, Kelley, & Grafton, 2009; associative sequence learning - Heyes & Ray, 2000). Furthermore, the goal-directed theory of imitation (GOADI) suggests that imitation is controlled through cognitive processes (Wohlschläger, Gattis, & Bekkering, 2003) which decompose the observed movement into a hierarchy of goals, with the primary goal driving subsequent action reproduction (Bekkering, Wohlschläger, & Gattis, 2000). The following review does not intend to debate these theories (see Heyes, 2011; Heyes & Bird, 2007), or discuss the evidence supporting OP. Thus, we will add to the current understanding of OP by reviewing the neural processes which underpin motor learning within the action-observation network. Following this, we review the contribution of bottom-up (stimulus-driven) and top-down (goal-directed) processes during OP. Finally, we suggest some implications for use in sport and motor learning settings, whilst providing possible research directions.

Motor learning within the action-observation network

Since the discovery of F5 mirror neurons in monkey (e.g., di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992) there have been over 100 studies examining the suggestion that a mirror mechanism is present in the human brain (see Caspers, Zilles, Laird, & Eickhoff, 2010). The first direct evidence was reported by Fadiga, Fogassi, Pavesi and Rizzolatti (1995), who measured motor-evoked potentials (MEPs) induced by transcranial magnetic stimulation (TMS) during the observation of upper-limb movements. The data indicated motor system excitation when an observer viewed another person making a movement, but more importantly that the MEPs were similar to those recorded during the execution of the same movement. Subsequently, it was shown that motor excitability was scaled and temporally linked to the observed kinematic events, such that a motor plan was constructed whilst the movement unfolded (Gangitano, Mottaghy, & Pascual-Leone, 2001). More recently, data from functional magnetic resonance imaging (fMRI) experiments have mapped the rostral part of the inferior parietal lobule (aIPL), pars opercularis of the inferior frontal gyrus (IFG), and adjacent ventral premotor cortex (vPM), as being the core mirror regions (MNS) during imitation (Iacoboni et al., 1999). In addition, it has been reported that the posterior part of the superior temporal sulcus (pSTS) is activated during action-observation (Iacoboni et al., 2001), although this region does not feature mirror properties. Together, these regions form the mirror-neuron circuit, or the action-observation network (AON) (Cross et al., 2009). The precise function of these regions has received much debate with suggestions that the pSTS supplies a visual description to the fronto-parietal mirror circuit, where IFG/vPM codes the goal-directed information (higher-level) and aIPL codes the motoric aspects of the movement (lower-level) (Iacoboni, 2005). However, there are data that indicate the frontal mirror regions code the kinematics, and the parietal mirror regions code the goal (see Hamilton, 2008).

Recent investigations have examined the role of this network during imitation learning (i.e., continuous process of observation followed by execution – also referred to as observational learning) and OP (i.e., observation across a series of trials featuring no motor execution). For example, Buccino et al. (2004) had participants observe (event 1), prepare (event 2) and execute (event 3) novel guitar chords during an fMRI experiment. They reported an increase in neural activity within the AON during observation (event 1) compared to rest (event 4). Subsequent imitation revealed activation in corresponding regions. Importantly, they also recorded activity in the dorsolateral prefrontal cortex (DLPFC) during preparation, which was interpreted as being the region that controlled the selection and re-configuration of pre-existing motor primitives into a novel representation of the observed act. Thus, these data presented a neural substrate linking sensorimotor processes associated with activating previously acquired motor representations (i.e., action recognition) and the acquisition of novel motor skills. Vogt et al. (2007) tested this hypothesis by manipulating the presence of learned or unlearned guitar chords after OP and showed that DLPFC activity was greater when observers viewed the unlearned guitar chords. In a follow up study (Higuchi, Holle, Roberts, Eickhoff, & Vogt, 2012), the activity recorded in DLPFC during OP positively correlated with the changes in motor performance (i.e., chord response times). Importantly, the authors reported functional connectivity between the DLPFC and AON, with the associated neural activity progressively decreasing as learners became more skilled at the task. Thus, at the skilled level, it would seem that more direct mirroring processes govern the relationship between action-observation and motor-execution (Calvo-Merino, Glaser, Grezes, Passingham, & Haggard, 2005). These data extend suggestions of sensorimotor transformations enabling motor learning through observation (e.g., Bird & Heyes, 2005; Mattar & Gribble, 2005), by incorporating higher-level supervisory control mechanisms.

Whilst the AON undoubtedly contributes to OP there are data that indicate the processes that operate during OP are not precisely the same as those involved during physical practice (Hayes et al., 2012; Higuchi et al., 2012; Ong & Hodges, 2010). For example, Ong and Hodges (2010) reported increased ‘after-effects’ (i.e., incompatible non-intended remnants of movement developed in a perturbed visuo-motor environment) for physical practice groups compared to a standard OP group. Furthermore, having first confirmed learning of a motor sequence timing task through OP or physical practice (Hayes et al., 2012), we found that only the physical practice group were able to successfully transfer to an intermanual *mirror* sequence condition (i.e., homologous motor commands - opposing visuo-spatial coordinates and effector). These differences can be explained by the addition of sensorimotor reafference from an operating effector(s) during physical practice. This reafference is compared to the predicted sensory consequences (forward model) in order to update and refine the sensorimotor representation (inverse model) developed during motor learning (see Elliott et al., 2010). Without sensorimotor reafference, the predominant source of information represented during observation is visual, which alters the comparison process. We do not suggest that this implies motor regions (e.g., primary motor cortex; premotor cortices; supplementary motor area) are not recruited during OP, but rather that a representation(s) developed through OP is primarily based on visuo-spatial codes as opposed to motor codes (e.g., Mattar & Gribble, 2005).

Bottom-up processes

A common indicator of bottom-up processing of the AON during observation is the implicit sensitivity to specialised visual information. Indeed, the AON preferentially responds to the observation of human stimuli, rather than non-human stimuli (see a review by Press, 2011 on the AON and biological tuning). Hence, the AON is thought to be biologically tuned, which makes sense given it develops through sensorimotor experience (Heyes, 2005) and underpins many socio-cognitive functions (Gallese & Goldman, 1998). From a motor learning perspective, the biological tuning of the AON may originate from connections to pSTS (Iacoboni, 2005), which is a region activated during the perception of biological motion (Bonda, Petrides, Ostry, & Evans, 1996). Thus, Iacoboni suggested that during OP, visual information projected from pSTS provides a visual description of the observed action to the frontoparietal mirror regions for subsequent action coding. Based on this suggestion, it is reasonable to predict that observing biological motion may facilitate the learning of novel motor skills.

Data from neurophysiological experiments confirm preferential coding of biological stimuli in the AON. For example, EEG data revealed increased interregional coherence of alpha-band activity in the frontoparietal central regions during the observation of finger movements (Holz, Doppelmayr, Klimesch, & Sauseng, 2008). Indeed, corresponding interregional coherence during observational learning correlated with performance accuracy scores of a novel finger sequence task (van der Helden, van Schie, & Rombouts, 2010). Moreover, it is not just the global properties of biological stimuli (e.g., human form) that tune the AON. For instance, the AON responds specifically to biological motion that adheres to normal kinematic laws such as the two-thirds power law of motion (Dayan et al., 2007; Casile et al., 2010). This latter finding is important as it indicates the AON encodes [ecologically valid] aspects of biological movements, which in the case of OP, may be the speed and temporal characteristics of complex motor skills.

Initial behavioural evidence to indicate biological tuning came from automatic imitation paradigms (Brass, Bekkering, Wohlschläger, & Prinz, 2000; Stürmer, Aschersleben, & Prinz, 2000), which examined stimulus-response compatibility in the presence of biological (finger movements) or non-biological stimuli (symbolic cues). Brass et al. (2000) reported finger lifting movements were initiated faster when the imperative stimulus cue was compatible with the model compared to viewing an incompatible model (e.g., finger tapping movement). This facilitation is thought to reflect automatic activation of motor codes that correspond to the observed action. Supporting this postulation is evidence of unintended movement deviation of arm movements when concurrently observing orthogonal human arm movements compared to robot arm movements (Kilner, Paulignan, & Blakemore, 2003). This effect was termed ‘motor contagion’ (Blakemore & Frith, 2005) based on the suggestion that the biological properties of the observed human movement directly activated a corresponding action representation within the observer’s motor repertoire.

In addition to stimulus-response and motor interference paradigms, the data from voluntary imitation experiments indicate that observers copy the movement kinematics (speed) displayed by a human model (Wild, Poliakoff, Jerrison, & Gowen, 2010) and biological-dot motion stimulus (Bisio, Stucchi, Jacono, Fadiga, & Pozzo, 2010). The latter effect shows that coding of biological motion is not limited to, or reliant upon, the presence of human form (Press, 2011). Thus, and irrespective of the stimulus type, it was suggested that movement kinematics are coded through lower-level mechanisms (e.g., direct-matching hypothesis; Rizzolatti, Fogassi & Gallese, 2001). We have found similar effects in our OP experiments involving motor timing tasks (e.g., Hayes et al., 2009). Specifically, movements initiated by observers produced similar kinematics (i.e., proportion of time to peak velocity and peak velocity) as those executed by the learning models (i.e., those that physically practised the motor timing task). In line with a direct-matching prediction, we suggested that motor timing could have been learned by coding biological motion through lower-level regions of the AON (i.e., bottom-up propagation based on motor resonance). However, because our task required learners to execute prototypical aiming actions (i.e., a simple upper limb movement directed to a target) the motor timing may have been influenced by higher-level goal-related processes (action-reconstruction hypothesis; Csibra, 2007). That is, both the model and observer may have coincidentally initiated the most efficient means to achieve a common goal (i.e., timing). It is noteworthy that the aforementioned voluntary imitation and OP studies differ to automatic imitation due to the additional processes influencing motor output (e.g., cognitive mediation). This has recently been recognised in the ideomotor model of imitation (Spengler, Brass, Kühn, & Schütz-Bosbach, 2010), where factors influencing perception (e.g., attention) and movement (e.g., inhibitory control) are suggested to mediate the automatic activation of sensorimotor representations (see Figure 5 published in Spengler et al. 2010).

Using a novel movement sequence timing paradigm, we have examined the potential confluence between the higher-level demands and motor constraints of the task by dissociating the timing goal (relative time) from the means of achieving the timing goal (Roberts et al., in prep). In a *natural* condition, participants observed a model displaying a prototypical aiming movement involving a relatively bell-shaped velocity profile (peak velocity occurred at ~50% of the movement). Meanwhile, the *unnatural* condition involved the observation of an atypical (but achievable) velocity profile (e.g., peak velocity occurred at ~95% of the movement). It is important to note that we kept the timing goal consistent across the two model conditions to examine whether observers learned the lower-level kinematics to subsequently obtain the timing goal, or emulated the timing goal by executing the most efficient means (i.e., not learning the *unnatural* kinematics). The data from a series of five experiments indicated that lower-level, *unnatural* biological motion was indeed learned. However, this process was not solely based on lower-level mechanisms in the motor system, but was also influenced by top-down processes associated with attention and hierarchical action coding. Thus, these data indicated that OP involves the contribution of both bottom-up and top-down processes, as opposed to a sole operating sensorimotor, or cognitive, mechanism.

The fact that coding of biological motion is subject to top-down, interpretative (human and point-light models) and higher-level processes supports the neurophysiological findings of similar levels of activity in the AON following observation of human and robotic reaching and grasping actions (Gazzola, Rizzolatti, Wicker, & Keysers, 2007). In addition, data recorded from aplasic participants, who born without hands, show increased activity in the AON during the observation of hand actions (Gazzola, van der Worp, et al., 2007). Interestingly, though, the region[s] activated was not an anatomical hand representation but rather an area responsible for executing either a foot and mouth action. It was therefore concluded the primary function of the AON was to code the goal of the action rather than the means in which the goal was achieved.

Consistent with the goal-matching properties of the AON is data collected from goal-directed imitation tasks where infants predominantly grasp the correct ear, but do so using an incorrect ipsilateral arm movement (Bekkering et al., 2000). However, when instructed to copy a similar contralateral arm movement with the goal to grasp an ear removed, participants successfully reproduced this arm movement (Gleissner, Meltzoff, Bekkering, 2000). These data underpin the GOADI theory, which states an observed action is decomposed into a hierarchy of task goals, with the primary goal being imitated at the expense of the means (Wohlschläger et al., 2003). Moreover, when end-state information is removed, the ‘means’ subsequently become the primary goal. Support for this model of OP was reported in a study by Hayes, Ashford and Bennett (2008) where school-aged children (10-11 years) successfully learned the means of an observed action in order to attain the outcome goal of a novel juggling cascade. That is, the necessity of the means can propagate certain action features up the action hierarchy and thereby facilitate motor learning.

Together, these data indicate the AON is not solely biased to automatically map biological motion onto the motor system during OP. Instead, it would seem to suggest that the AON responds to an observed action at multiple levels by engaging bottom-up (stimulus-driven, motor resonance) and top-down (goal-directed, inferential, attention) processes.

Top-down modulation

The confirmation that top-down factors influence action-observation has been reported in tasks that have manipulated attention (Bach, Peatfield, & Tipper, 2007), context (Liepelt, von Cramon, & Brass, 2008) and belief (Liepelt & Brass, 2010; Stanley, Gowen, & Maill, 2007). For example, the unintended movement deviation (i.e., motor contagion) reported during concurrent observation of orthogonal dot-motion displays was enhanced when participants were informed the stimuli were human-generated compared to computer-generated (Stanley et al., 2007). These effects were independent of the velocity characteristics (i.e., two-thirds power law or constant velocity) of the dot motion and indicate that the system responsible for processing biological motion can also be engaged through the human interpretation (i.e., belief) of an inanimate point-light dot. Moreover, even when controlling the perceptual similarity between the stimulus and the effector operated by the observer, the attribution of human movement via belief continues to prime the motor system during automatic imitation (Liepelt & Brass, 2010). This led to the ‘gating hypothesis’, which predicts observed stimuli believed to be biological gains privileged access to the AON. The aforementioned effects indicate that motor contagion and/or automatic imitation are not default behaviours independent of higher-level cognitive processes.

A neural substrate for these top-down processes has been proposed based on the inhibition of automatic imitation in frontal lesion patients (Brass, Derrfuss, Mathes-von Cramon, & von Cramon, 2003). Neuro-imaging data indicate the anterior frontomedian cortex (aFMC) and temporo-parietal junction (TPJ) provide top-down control (Brass, Derrfuss, & von Cramon, 2005). Moreover, these top-down processes have been shown to mediate bottom-up processes during action-observation (Spengler, von Cramon, & Brass, 2010). Therefore, given the similarity in the mechanisms forwarded in sensorimotor models of imitation learning (Buccino et al., 2004), OP (Higuchi et al., 2012) and automatic imitation, it is reasonable to predict top-down processes may impact motor learning by observing. Therefore, future research on OP should examine whether top-down processes modulate bottom-up processes in a motor learning context.

In addition to top-down control, the aforementioned neural regions may also support mentalizing functions (Frith & Frith, 2003). This was demonstrated in recent behavioural (Leighton, Bird, Orsini, & Heyes, 2010; Wang, Newport, & Hamilton, 2011) and neurophysiological (Wang, Ramsey, & Hamilton, 2011) experiments, which manipulated social cues/primes. For example, Leighton et al. (2010) conducted a two-part experiment where participants first completed a social priming task followed by an automatic imitation task. The priming task involved reading and constructing sentences from words that encouraged a pro-social attitude (e.g., *cooperate or team*) or an anti-social attitude (e.g., *alone or enemy*). The data showed a robust motor priming effect featuring faster response times following a pro-social prime compared to an anti-social prime. A similar manipulation revealed enhanced motor priming following a direct gaze condition (eye gaze of model directed towards observer), compared to an averted gaze condition (eye gaze of model directed away from observer) (Wang, Newport, & Hamilton, 2011). These effects were related to activity of medial prefrontal cortex (mPFC), STS and IFG, including a functional connectivity between mPFC and STS (Wang, Ramsey, & Hamilton, 2011). Although there is no evidence to indicate social cues/primes regulate OP, these data indicate that the top-down processes mediating bottom-up mechanisms are closely linked to social functions. Thus, we are currently exploring this issue using a social priming paradigm (e.g., direct or averted gaze) in which participants are required to learn a novel aiming movement that contains *unnatural* (experimental condition) or *natural* (control condition) movement kinematics. We predict that participants will learn the *unnatural* kinematics more accurately in the *direct* condition because eye gaze will impact the top-down processes (mPFC) and subsequently mediate the bottom-up mechanisms required for coding the *unnatural* biological motion.

Conclusion

A review of neurophysiological and behavioural literature related to OP, indicates that this process is mediated by a mirror mechanism located in aIPL and IFG/vPM. Together, these neural regions make up part of the AON, which in combination with working memory processes located in DLPFC, can develop novel motor representations. Rather than simply being sensitive to biological stimuli (bottom-up processes), it is now recognised that the AON also responds to non-biological stimuli if preceded by primes that influence belief or social belonging (top-down processes). In this way, the bottom-up processes operating during OP can be modulated by top-down processes. Hence, sport scientists, coaches and educators should consider the interaction of bottom-up and top-down processes during the design and implementation of OP. Specifically, the emergence of an overlap between mentalizing and top-down functions means the manipulation of social (social cues; instructions) or contextual information may influence bottom-up processing of biological motion in order to facilitate the acquisition of motor skills.

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